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THE SPATIAL PATTERN ON NEST
AND THE POPULATION DYNAMICS OF
Polyrhachis vicina ROGER
(Hymenoptera: Formicidae)

Wang Jinfu

(Institute of Parasitic Diseases, Zhejiang Academy of Medical Sciences, No. 60, Tian Mu Shan Road,
Hangzhou, Zhejiang 310013, P. R. China)

Tang Jue

(Department of Plant Protection, Zhejiang Agricultural University, Hangzhou, Zhejiang 310029,
P. R. China)

Abstract The nest spatial pattern and the colony caste composition of *Polyrhachis vicina* Roger were measured.

1. Nests were regularly spaced from January to June or from September to December, randomly spaced in July and aggregated in August.

2. In the cold season, nests were built at the place where could acquire solar radiation. In the warm season, most of nests were built in the shade.

3. The population of the ant grew from the winter to the summer and descended gradually after the early autumn. Eggs, larvae, workers, queens and males existed yearly in the nest. Pupae appeared for 8 months from April to November and peaked in August. Gynes were present in the autumn.

Key words *Polyrhachis vicina*, Ant, Spatial pattern of nest, The nearest distance method, Population structure

Polyrhachis vicina Roger is a robust and black ant of Asia, which lives in the clump of bushes or arbors on hillsides where the major plant is *Pinus massoniana* Lamb., *Quercus fabri* Hance, *Arundinella setosa* Trin and so on. A population, from Yongkan, Zhejiang of China, comprised polygynous colonies that generally had queens, females, males, larvae, pupae, eggs and workers (Chen et al., 1989). Some of these castes presented yearly and others presented only in some season. The size of colony was various as time went on. Most of colonies may move to a new site to build a new nest once each season and a smaller number of colonies will relocate a second time.

本文 1995 年 3 月 15 日收到, 同年 7 月 25 日修回

In this paper, we intended to measure the spatial distribution of *P. vicina* nests and the size of its colony in the fields in order to illustrate the dynamics of the spatial and temporal patterns of the ant population, which included the variation of spatial pattern of ant-nests, the interaction between the nest relocation and the environment factors, and the variation of population structures.

1 Methods

All of detailed observations were carried out in Yongkan, Zhejiang Province in 1989–1991. Three study sites were representatively selected on three hillsides in which the vegetation was bushes, arbors and grasses, such as *P. massoniana*, *G. fabri*, *Smilax china*, *Ilex cornuta*, *Rosa bracteata*, *Symplocos caudata*, *Vitex negundo*, *Glochidion puberum*, *Lespedeza formosa*, and *A. setosa*. The main food exploited by the ant was the honeydew secreted by the aphid *Lachnus tropicalis* and the scale *Matsucoccus* spp., the secretion of pine trees, or the small insects (Wang *et al.*, 1994). The investigation was made once a month.

1.1 Nest distribution

All of ant-occupied nests in three study sites were marked with the wood tags on which the date of the nest-establishment and its serial number were recorded. Those nests which had been abandoned by the ants would be removed their tags and the new nest would be marked every month. We measured distances between nests in the study site with the tape and analyzed the spatial pattern of ant-nests by the nearest distance method developed by Clark *et al.* (1954). If, in a site of N nests having a specified density ρ , the distance r from each nest to its nearest neighbor is measured, the mean observed distance may be represented as $\bar{r}_A = \sum r / N$. The mean distance to nearest neighbor which would be expected if these nests were distributed at random, \bar{r}_E , can be shown to have a value equal to $1 / (\alpha * \sqrt{\rho})$. The ratio $R = \bar{r}_A / \bar{r}_E$ can then be used as a measure or degree to which the observed distribution approaches or departs from random expectation. In a random distribution, $R=1$, Under conditions of maximum aggregation, $R=0$. In an even distribution, $R>1$.

The measured area of every study site was determined by the range of vegetation distribution in the study site, specially *P. massoniana*, *G. fabri* and *A. setosa*. Usually these plants distribute in patch on hillsides and ant-nests are established in the area of the plant patch which is surrounded by the bare rock, never beyond it. The measured area of study site was 223.66 m² for site No. 1, 1299.30 m² for site No. 2, and 76.80 m² for site No. 3.

1.2 Population structure

In the middle ten days of every month we sampled 9–12 colonies of *P. vicina* from three sites beyond those study sites mentioned above. Before being excavated, these colo-

nies were anesthetized with the ether for 5–10 min. Then they were excavated and carried into the insectarium for dissection. From December to the next March, only queens, males, eggs and larvae presented in the colony, pupae existed from April to November and females from September to November. The average size of colony for each month could be estimated and apportioned between the castes.

In order to illustrate the dynamics of population of the ant, we calculated relative parameters between densities of castes to establish the relative matrix (M) of caste structure of the colony. Then the tendency of population development was analyzed with the Fuzzy Assemble Analysis (Zhao *et al.*, 1984):

$$M^k = M^{2k} = M^* \quad (1)$$

Where k is the even number, M^* is the Fuzzy equal matrix. Finally, the dynamics of population of the ant was shown by the dendrogram.

2 Results

2.1 Spatial pattern of ant nests and its tendency

The spatial pattern of ant-nests could be measured and analyzed because each nest fixed in some place, although this fixed distribution was comparative to a certain time. The colony usually abandoned its old nest and built its new nest in another place. Some of larger colonies may be divided into two or more small colonies which would build their respective nests, or several small colonies would be merged into a larger colony. The spatial pattern of ant nests varied as season went on. With the nearest distance method used often in the plant ecology, the spatial pattern of ant-nests in each month was shown as Tab. 1.

For the comparison between three study sites, R of site No. 1 was the smallest and that of site No. 3 was the largest. It was relative to the number of nests in the study site or to the spatial distance between these nests. The density of nests ρ or the average nearest distance \bar{r}_A in site No.2 was smaller or larger than that in site No.1. In site No. 3, although its density of nests was larger than that in site No.1 sometimes, its average nearest distance \bar{r}_A or the nearest distance expectation \bar{r}_E was much larger or much smaller than that in the latter. Thus, the spatial pattern or nests in site No.1 was the most aggregative.

The average aggregation parameters from three study sites were used to analyze the variation of spatial pattern of ant nests (Tab. 2). Those distributions of nests from January to June and from September to December were the even patterns ($R > 1$). The aver-

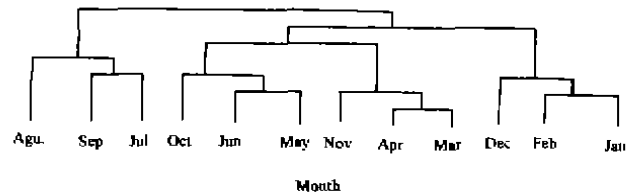


Figure 1 The dendrogram of dynamic assembly of a colonial population. The lower their joint line, the more similar their colonial caste compositions

Table 1 Parameters of spatial pattern of ant-nests

Month	Site	m^2	N	ρ	$\sum r$	\bar{r}_A	\bar{r}_E	R
Jan	1	223.66	12	0.0537	43.97	3.6638	2.1571	1.6980
	2	1299.30	12	0.0092	124.57	10.3810	5.2129	1.9914
	3	76.80	3	0.0391	36.33	12.1092	2.5286	4.7889
Feb.	1	223.66	11	0.0492	32.26	2.9325	2.2542	1.3009
	2	1299.30	13	0.0100	110.32	8.4865	5.0000	1.6973
	3	76.80	4	0.0521	40.29	10.0732	2.1905	4.5986
Mar.	1	223.66	12	0.0537	31.53	2.6279	2.1577	1.2179
	2	1299.30	14	0.0108	110.73	7.9093	4.8113	1.6439
	3	76.80	5	0.0651	33.01	6.6012	1.9597	3.3685
Apr.	1	223.66	19	0.0850	33.16	1.7450	1.7150	1.0175
	2	1299.30	16	0.0123	114.14	7.1339	4.5083	1.5824
	3	76.80	5	0.0651	21.75	4.3501	1.9597	2.2198
May	1	223.66	23	0.1028	35.56	1.5459	1.5595	0.9913
	2	1299.30	17	0.0131	109.61	6.4479	4.3685	1.4760
	3	76.80	6	0.0781	18.09	3.0166	1.7891	1.6861
Jun.	1	223.66	22	0.0984	33.90	1.5411	1.5939	0.9660
	2	1299.30	17	0.0131	99.02	5.8245	4.3685	1.3333
	3	76.80	6	0.0781	14.85	2.4752	1.7891	1.3835
Jul.	1	223.66	23	0.1028	26.23	1.1406	1.5595	0.7314
	2	1299.30	19	0.0146	84.59	4.4521	4.1380	1.0759
	3	76.80	7	0.0911	13.62	1.9452	1.6566	1.1742
Aug.	1	223.66	24	0.1073	12.46	0.5193	1.5264	0.3402
	2	1299.30	20	0.0154	79.95	3.9973	4.0291	0.9921
	3	76.80	8	0.1042	13.30	1.6631	1.5489	1.0737
Sep	1	223.66	24	0.1073	33.76	1.4066	1.5246	0.9215
	2	1299.30	16	0.0123	82.42	5.1512	4.5083	1.1426
	3	76.80	6	0.0781	16.89	2.8148	1.7891	1.5733
Oct.	1	223.66	21	0.0939	39.66	1.8887	1.6317	1.1575
	2	1299.30	15	0.0115	108.18	7.2120	4.6625	1.5468
	3	76.80	6	0.0781	19.44	3.2408	1.7891	1.8114
Nov.	1	223.66	18	0.0805	45.84	2.5467	1.7623	1.4451
	2	1299.30	14	0.0108	104.47	7.4623	4.8113	1.5510
	3	76.80	5	0.0651	19.38	3.8763	1.9597	1.9780
Dec	1	223.66	13	0.0581	39.15	3.0119	2.0743	1.4520
	2	1299.30	12	0.0092	98.76	8.2296	5.2129	1.5787
	3	76.80	4	0.0521	22.42	5.6061	2.1905	2.5593

m^2 =the area of study site, N =the number of nests, $\rho=n/m^2$, $\sum r$ =the sum of nearest distances,

$$\bar{r}_A = \sum r / N, \quad \bar{r}_E = 1 / (\alpha * \sqrt{\rho_{21}}), \quad R = \bar{r}_A / \bar{r}_E.$$

age aggregation parameter (R) in July was 0.9938 which approximated to 1 and its spatial pattern could be regarded as the random. The spatial pattern in August was

aggregative ($R=0.808 < 1$).

There was a significant correlation ($r=-0.9483$; $P<0.01$) between the average aggregation parameter (R) and the average density of ant-nests ($\bar{\rho}$) for every month (see Tab. 2) as following:

$$R = 3.9235 - 42.0271\bar{\rho} \quad (2)$$

The equation (2) showed that the average aggregation parameter of nests was negatively correlated with the average density of nests in the study site. We deduced $\bar{\rho}_1 = 0.0933$ (no./m²) when $R=0$ and $\bar{\rho}_2 = 0.0696$ (no./m²) when $R=1$ from the equation. In this region, the aggregation of nests would intense as $\bar{\rho}$ increased. Nests would be even distributed ($R>1$) when $\bar{\rho} < \bar{\rho}_2$, and nests would be super-aggregated ($R<0$) and spatial competition would sharpen greatly when $\bar{\rho} > \bar{\rho}_1$. The tendency of spatial patterns of nest was that nests scattered sparsely in the field in the cold season would be aggregated gradually as the climate warmed and the food resources increased, being most aggregative in August, and then dispersed as season went further no, being sparest in January.

Table 2 The parameters of environmental conditions of nest distribution

Month	R	$\bar{\rho}$	SE(%)	SA(%)	FN(%)	BN(%)	GN(%)	PN(%)	RD(m)	PD(m)
Jan.	2.8261	0.0340	100	3.70	29.63	22.22	70.37	7.41	1.95	1.45
Feb.	2.5323	0.0368	100	0	11.11	7.41	85.19	7.40	1.06	1.45
Mar.	2.0768	0.0432	100	0	16.13	12.90	87.10	0	1.71	2.24
Apr.	1.6066	0.0541	100	0	10.00	12.50	82.50	5.00	1.14	2.41
May	1.3845	0.0647	100	0	10.87	8.70	91.30	0	2.71	1.22
Jun.	1.2279	0.0632	91.11	48.89	42.22	66.67	33.33	0	2.63	0.99
Jul.	0.9938	0.0695	97.96	95.92	81.63	10.20	42.86	46.94	3.14	0.52
Aug.	0.8020	0.0756	100	94.23	84.62	57.69	5.77	36.54	3.37	0.15
Sep.	1.2125	0.0612	100	91.30	80.43	47.83	19.57	32.60	2.25	0.47
Oct.	1.5052	0.0612	100	42.86	38.09	47.61	16.67	35.72	1.94	0.73
Nov.	1.6580	0.0512	100	13.51	27.03	27.03	59.46	13.51	1.07	0.90
Dec.	1.8633	0.0398	100	6.90	20.69	13.79	79.31	6.90	1.21	1.17

R = the average aggregation index; $\bar{\rho}$ = the number of nests / m²; SE = the percentage of southern exposed nests; SA = the percentage of sunshade nests; FN = the percentage of nests built in the pine forest; BN, GN or PN = the percentage of nests built at feet of bush, at feet of grass or on tops of pine trees; RD or PD = the distance from the nest to the rock around or to the pine forest

2.2 Interaction between the nest distribution and the environmental factor

Colonies may relocate thier nests in different habitats to adapt for various environmental factors, specially of the air temperature and the food condition (Wang *et al.*, 1994). The environmental conditions of nest distribution were measured and count-

ed as Tab.2.

For the exposure direction, most of nests were exposed to the south, specially in the microthermal season when all of them were in the southern exposure, but a few of nests in the summer occasionally were exposed to the north. In the megathermal seasons, most of nests were built in sun-shading places, for example, some of them were covered by the thick foliages of bush or by the dense grasses. The sun-shading ratio in Tab. 2 is the percentage of sunshade nests in total nests. It started to increase in June and was highest in August, but it decreased in the microthermal season, even some of nests were almost exposed completely.

The pine forest in the study site was separated from the rock around by a narrow section of grasses. We measured the percentage of nests in the pine forest and distances between each nest and the forest (it was 0 for those nests built in the forest) as well as the rock around (Tab. 2). Most of nests in the cold season were distributed out of the forest and were nearby the rock. As the air temperature increased, nests moved gradually toward the forest and their distances would decrease though some of nests would still be relocated out of the forest.

The nest location was the foot of bush or grass, or the top of pine branches growing for 3-4 years. The percentages of nests distributed at these locations were changed with season. The colony built its nest mostly at the foot of withered grass in the spring or the winter and moved its nest into the foot of bush, even some of nests would be built at the top of pine with dense conifers. In July and August, about one-thirds of nests were built at the top of pine.

2.3 Caste structure of colony and its dynamics

Although individuals would exchange occasionally between colonies (Chen *et al.*, 1989, 1990), the size of every colony was stabilized in a given time. The population of a colony was used to analyze the caste structure and its dynamics (Tab. 3).

The population structure of *P. vicina* colony was the different combination of queens, males, gynes, eggs, larvae, pupae and workers. The gyne only presented in the duration from September to November, specially in October, so that the life cycle of the ant was one generation for one year. The gyne was going to mate with the male soon after its eclosion and then took off its wings to become the queen. The density of queen, therefore, reached its climax in October. The reason of the queen density decreased in November, being roughly inferred, may be that a large number of old queens died. The worker was the important caste in the colony and completed all its development in about two months in the suitable seasons. The proportion of worker in the colony was highest all along. The worker density of January was least and then increased gradually until August when it was most abundant. After that time it began to decrease till the next January. Unlike the gyne, the male developed in the spring and the autumn according to the observation in the insectarium. For this reason, the male densi-

ty had two climaxes in the Tab. 3, one in the spring (April) and another in the autumn (October). The pupa was also not presented yearly. That no any pupa existed in the colony in the winter may be the cause of larva diapause in this season. As the winter came up, those pupae in the autumn had emerged into workers or sexual adults and those larvae began to diapause gradually till their development and pupation in the next spring. The pupa only presented from April to November.

Table 3 Average sizes and structures of natural colony (No. / Per colony)

Month	T	W	Q	M	G	E	L	P
Jan	5590.6	4526.6	29.9	98.1		41.9	894.1	
Feb	6520.6	6182.8	24.8	33.3		195.6	144.1	
Mar	7803.6	7491.5	19.5	48.3		156.1	88.2	
Apr.	7503.4	6453.0	47.3	393.9		243.8	356.4	9.0
May	8404.3	5210.9	31.0	273.1		1239.6	357.2	1292.5
Jun	8254.6	4045.8	37.1	4.1		1031.6	990.3	2145.7
Jul	10127.3	7088.9	30.3	20.2		354.5	1342.0	1291.4
Aug	14859.5	6688.5	37.1	371.4		965.6	3937.0	2859.9
Sep	11635.0	5936.8	58.0	509.4	4.7	1104.8	2936.3	1085.0
Oct	7985.2	4226.8	119.7	638.4	167.5	738.1	698.2	1396.5
Nov.	6456.9	5295.5	38.7	387.1	3.3	64.5	467.7	200.1
Dec.	6060.7	4547.1	24.2	218.0		181.6	1089.8	

T=the total population of a colony, W, Q, M, G, E, L or P=the number of workers, queens, males, gynes, eggs, larvae or pupae respectively in a colony.

The population structure of colony varied significantly between months. By the relative parameters between caste densities and the Fuzzy Assemble Analysis, its variation could be divided into four stages (Fig. 1): the first stage was the duration from November to the next February when the size of colony was least and no any pupa and gyne presented; the second stage was the duration from March to June when the size of colony began to increase, the pupa presented, and the male density reached the first peak; the third stage was the duration from July to September when the populations of colony, pupa, larva, and egg were most abundant and a few of gynes emerged; the duration of October and November was divided from the second stage (see Fig. 2), and classified into a single stage, i. e. the fourth stage because its characteristic was that a large number of gynes emerged and the male density reached the second peak, it could be named as the sexual stage.

3 Discussion

For *P. vicina*, the aggregation and the density of nests and the size of each colony

increased in the summer and decreased in the winter. There appeared to be a strong variation trend with season and to be the significant interactions between these indexes (the relative parameter (r) of the aggregation (R) and the density of nests $\bar{\rho}$ (no./m²) was -0.9483, that of the aggregation (R) and the size of colony (T) was -0.7736 (by regression analysis for R in Tab. 2 and T in Tab. 3), and that of the number of nests and the size of colony was 0.8053 (by regression analysis for $\bar{\rho}$ in Tab. 2 and T in Tab. 3). This negative correlation is contrary to observations of Cushman *et al.* (1988) and Ryti (1990) who found a positive correlation of R and density. The observation method was similar. In *P. vicina*, it may be interpreted by the fact that some of newly increased nests in summer are really satellite nests within a main colony and they were located near the "parent" nest. This fact was different from that of ant species observed by Cushman *et al.* and Ryti.

Nest relocation in a given area would be of obvious advantage to a colony as it assures that the new nest site will be located in an area of minimal pressure from neighboring colonies and adequate food resources (Harrison *et al.* 1981). *P. vicina* has its particularity. In the warm season that was main time for the ant to forage its foods, some of individuals from a larger colony built satellite nests near the "parent" nest or whole of a colony from its old nest moved to build its new nest, which resulted in a high density of nests and an aggregative pattern of nest distribution. Another cause of high nest density in this season was that there were a lot of food resources which reduced the intraspecific competitive pressure for foods. In cold seasons, some of smaller colonies merged into a larger colony in order to improve the microclimate in the nest. Consequently, the density of colonies would be decreased and nests in a given area were distributed sparsely.

There is a strong selection pressure on the size of the colony needed for a species to make the best use of its habitat. The average size of a *P. vicina* colony may be determined by its biological specificities and the food richness available per unit area. The spring was an important season of colony production. As it warmed, a large number of worker individuals were produced and the size of each colony would be increased rapidly. Any individual colony would grow to a size limited by its nest capacity. If it was over-crowded, the colony would be divided into two or more smaller colonies which were still larger than those in the winter. Therefore, we inferred that the production of new queens increased the density of colonies while increasing the size of a colony. New queens emerging in the autumn may be stayed in the same nest till the next spring when they produced a large number of offsprings so as to enable a colony so over-crowded that it was disrupted into several smaller colonies. The cold reasons resulted in the reduction of available foods in the field and the death of individuals that led to the decrease of colony size and the drop of temperature in the nest. In order to raise their foraging efficiency and to improve the microenvironment in the nest, these smaller

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colonies would merge into some larger colonies which were still smaller than those in the summer.

Acknowledgements The authors wish to thank Prof. Cheng Jaan and Dr. Liu Shusheng for critical review of this manuscript, and are grateful for helpful suggestions offered by Prof. Li Sheng. All of investigations were assisted by Mr. Hu Jiehua and his colleagues.

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鼎突多刺蚁蚁群的空间和时间动态

王金福

(浙江省医学科学院寄生虫病研究所 310013)

唐 觉

(浙江农业大学植物保护系 310029)

Q969.554.2

A 摘要 本文对鼎突多刺蚁野外群体的空间格局、蚁群品级结构及其时间动态等方面作了研究。

1. 野外蚁群在 1 月至 6 月和 9 月至 12 月期间表现出均匀分布的格局, 7 月期间为随机分布型, 而 8 月份则是聚集分布。

2. 在较冷的季节, 其蚁巢往往建立在那些朝南向阳的地方, 以使其蚁巢能获得更多的热能; 在炎热季节则把蚁巢建立在尽可能遮阴避阳的地方。

3. 蚁群的种群从初春开始逐渐增长, 至夏季达高峰, 初秋后又逐渐下降。蚁群中卵、幼虫、工蚁、蚁后和雄成虫全年都存在; 而蛹只在 4 月份至 11 月份的 8 个月中出现, 并在 8 月份达高峰。有翅雌蚁仅在秋季出现。

关键词 鼎突多刺蚁, 蚂蚁, 蚁巢空间格局, 最近距离法, 种群结构